The Pan-Pacific Entomologist

Vol. 42 JANUARY 1966 No. 1

Observations on the Floral Relationships of the Galápagos Carpenter Bee[1]

(Hymenoptera : Apidae)

E. G. LINSLEY, C. M. RICK, AND S. G. STEPHENS[2]

The Galápagos carpenter bee, *Xylocopa darwini* Cockerell, was not named and characterized until 1926, although its presence in the archipelago was reported as early as 1887 by Frederick Smith under another name. The status of the species has been discussed by Hurd (1958b) and its recorded distribution in the islands summarized by Hurd (1958b) and Linsley (1966). Nothing was known of its floral relationships until Rick (1963) reported sporadic visits to the Galápagos tomato, *Lycopersicum pimpinellifolium*, and more intense activity about plants of the genera *Piscidia, Momordica,* and *Cryptocarpus.* Subsequently, in the course of a study of some plant–animal relationships in the Galápagos, he has recorded *X. darwini* as a pollen vector of *Castela galapageia, Cardiospermum galapageium, Opuntia echios, Cordia lutea, Periloba galapagensis, Justicia galapagana, Scalesia affinis,* and *S. helleri* (Rick, 1966), all but one of these being endemic.

Up to the present time, honeybees are not established in the Galápagos, attempts to introduce them having failed—presumably as a result of predation by mockingbirds. Only one species of bee, *Xylocopa darwini,* has been formally reported from the islands, although from local residents we heard reports of the so-called "dwarf bee of Floreana." We did not encounter it in any of our transects of that island made during February, and tentatively concluded that if there is indeed another species of bee on Floreana, it must be rare, or localized, or active at some other season.

In any event, the Galápagos carpenter bee, *Xylocopa darwini* Cockerell, is undoubtedly the principal pollen vector associated with plants of the Galápagos flora. Both males and females transport significant amounts of pollen on their body hairs as they move from

---

[1] Contribution No. 29 from the Charles Darwin Foundation for the Galápagos Islands.

[2] University of California, Berkeley; University of California, Davis; and North Carolina State University, respectively.

THE PAN-PACIFIC ENTOMOLOGIST 42: 1–18. January 1966

flower to flower in search of the nectar required to sustain them in their adult life, and the females systematically collect and store pollen for the immature stages of the next generation. Insect competitors for pollen are few—mainly beetles. Competitors for nectar, though more numerous, are limited largely to a few species of butterflies, moths, wasps, and flies (Linsley, 1966).

ORIGIN OF THE GALÁPAGOS CARPENTER BEE

Little may be said with confidence about the origin of the Galápagos carpenter bee beyond the fact that it belongs to the exclusively New World subgenus, *Neoxylocopa*, a very large group, the systematics of which are poorly understood (Hurd and Moure, 1963). However, when the relationships of its meloid parasite of the genus *Cissites* have been determined, they may shed some light on this problem, since its habits are such as to make it extremely unlikely that it arrived in the archipelago independently of its host.

Hurd and Moure (1963) have commented that "although a number of the Pacific oceanic island groups seem to offer suitable environmental conditions for occupancy by at least certain species of the genus *Xylocopa*, relatively few have been successfully invaded. In the eastern Pacific only two, the Galápagos Islands, situated on the equator, 650 miles west of the Ecuadorean coast, and the Revillagigedo Islands, located between 400 and 600 miles off the western Mexican coast near 18° N. and 112° W., have been occupied. In both of these archipelagos the genus is represented by a single species. Interestingly, these species, as well as the Hawaiian and Marianas islands adventive, belong to the chiefly Neotropical subgenus *Neoxylocopa*. All three species appear to have established themselves within historic times, though very possibly *Xylocopa darwini* Cockerell of the Galápagos Islands may have become adventive much earlier (Hurd, 1958b:250, 251). It is curious that no species of other New World subgenera of the genus *Xylocopa* are known from any of the islands of the eastern Pacific, including the continental islands."

Perkins (1899), who first studied the habits of the Hawaiian carpenter bee in any detail, believed it to have been imported by man in lumber, but at the same time he pointed out that its habits are such as might have enabled it to reach the islands by natural immigration, for it is particularly fond of breeding in dead logs on the seabeaches, especially in the very light, dry logs of *Erythrina*.

While all agree that the Hawaiian carpenter bee is adventive, having been identified with an American bee currently known as *Xylocopa* *brasilianorum sonorina* Smith (see Hurd, 1958b for references), it should be pointed out that the Galápagos carpenter bee, *X. darwini* Cockerell, and the Revillagigedo carpenter bee, *X. clarionensis* Hurd, have not yet been identified with mainland species or subspecies. Our field studies, although preliminary and incomplete, suggest that the Galápagos carpenter bee may have been in the archipelago for a relatively long time, although not so long as the older elements of the endemic flora (see below).

BASIC ECOLOGICAL REQUIREMENTS OF THE CARPENTER BEE

The Galápagos carpenter bee, like its relatives elsewhere, has three basic requirements which must be met in order to sustain the population, regardless of how otherwise favorable or hostile the physical and biotic environment in which it lives may be. These are (1) a source of food (principally nectar) to sustain the adults during the active period of their lives, (2) a suitable substrate (wood) in which to construct the burrows and cells in which the young develop, and (3) a source of food (pollen and nectar) which can be stored for the larvae, since the larvae cannot forage for themselves. The habits of carpenter bees in general have been summarized by Malyshev (1931), Hurd (1958a) and Hurd and Moure (1963).

Although our principal concern in this report is with those activities of carpenter bees involved in attempts to meet the first and third of these requirements, it should be mentioned that on most of the islands where carpenter bees were observed, availability of suitable nesting substrate did not appear to be a limiting factor. There was an abundance of dead wood, both standing and fallen, especially *Bursera graveolens* and *Croton scouleri* which are commonly used for nesting. Williams (1926) reported that Galápagos carpenter bees were using these same species for nesting in 1905–1906, along with *Hibiscus tiliaceus*, but he emphasized especially their use of the very soft wood of *Erythrina velutina*. We found carpenter bees nesting in all of these plants, as well as in *Scalesia affinis*, *Castela galapageia*, and *Maytenus obovata*. However, we did not find them utilizing agave, as reported by Garth (1933). As generally reported for other carpenter bees, their nest burrows run with the grain and thus are vertical in standing dead wood, horizontal in fallen logs and branches.

FLOWER-VISITING HABITS OF THE GALÁPAGOS CARPENTER BEE

The Galápagos carpenter bee as a species is polylectic and visits a wide variety of plants in search of pollen as well as nectar (60 of these plant species, representing 28 plant families, are enumerated in Table 4). However, at various times of day, depending upon availability of pollen or nectar, individual bees may concentrate their activity on a single species of plant. For example, on Santa Cruz Island during January and February 1964, a favored early morning nectar source in the lowland areas near the beach was *Hibiscus tiliaceus* (Malvaceae), a flowering shrub or tree which, at least in the vicinity of Academy Bay, does not appear to produce pollen. Along the trails to the highlands, in the arid and transition zones, a favored early morning nectar source was *Boerhaavia scandens* (Nyctaginaceae), a weedy species with clusters of small flowers. This plant has long, slender, tough peduncles which bend under the weight of the bee, so as to invert the flowers, but do not break. The bees work each flower in a cluster, flying from one to another quickly and alighting on the next flower before the stem, which springs back when relieved momentarily of the weight of the bee, is fully erect. Although the bees appear to be attracted to this plant primarily for nectar, captured individuals frequently had small amounts of pollen packed into the hairs of the posterior basitarsi. Growing near patches of *Boerhaavia*, scattered plants of *Bacopa moniera* (Scrophulariaceae) were often visited for nectar at the same time. Bee samples from this plant had no pollen on the basitarsi. On several occasions it was noted that bees taking nectar from *Bacopa* were constant to it, those taking nectar from *Boerhaavia* constant to it. None were seen to switch plants, but they undoubtedly do so on occasion. However, the most abundant flowering plant along the trail, *Portulaca oleracea*, also a weedy species, did not appear to be visited by bees in spite of the yellow flowers. *Boerhaavia* flowers are pink to our vision, *Bacopa* flowers, white; they must also appear different to the bees in order to permit the flower constancy observed in mixed populations.

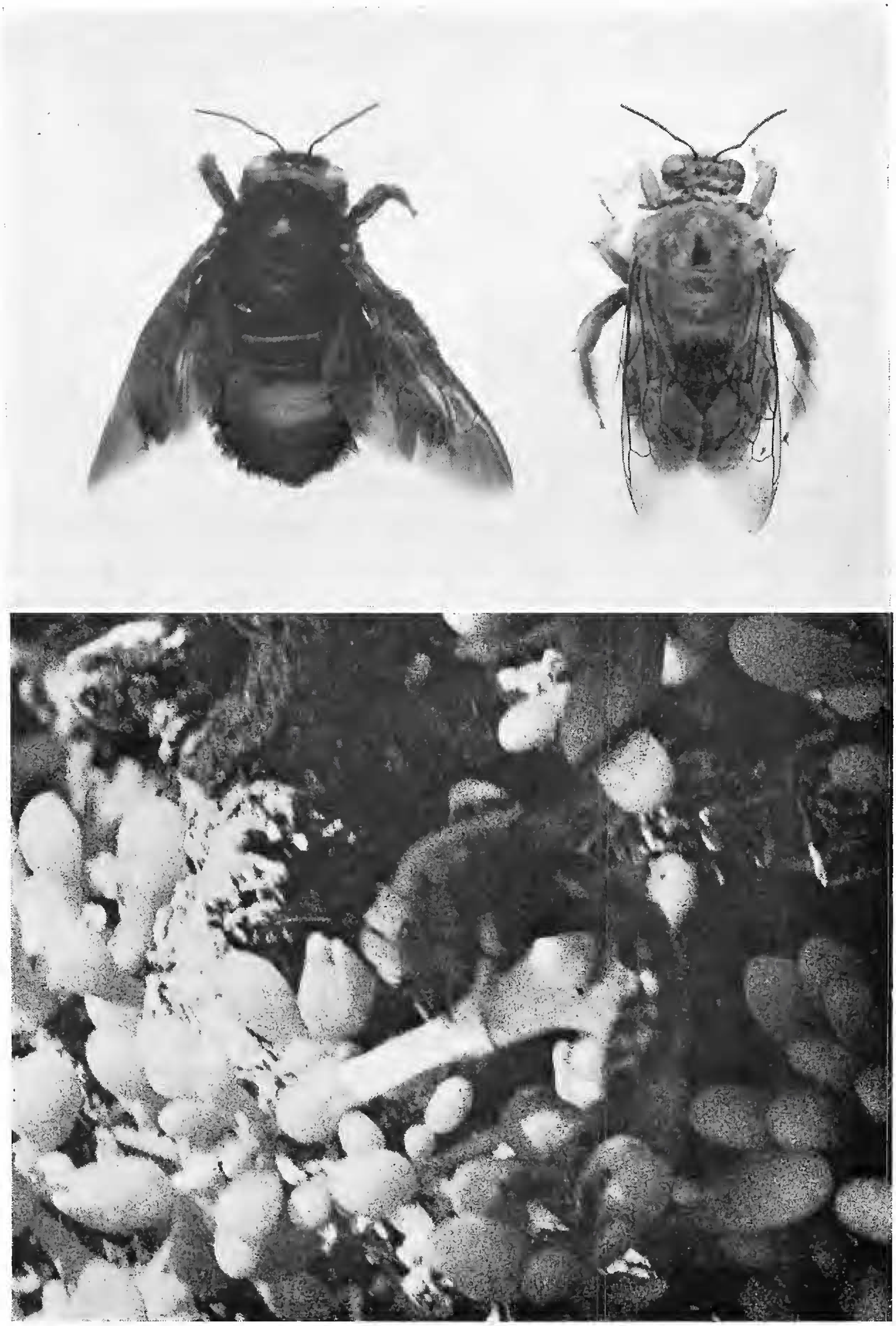
As the day progresses other sources of nectar are utilized—as would be expected—and this sequence will not be detailed here since no doubt it varies from season to season and certainly differs from place to place (*e.g.*, Santa Cruz vs. Floreana Islands). However, two special situations may be mentioned. The shrub *Clerodendron molle* has white flowers with a deep, narrow corolla tube, four long exposed stamens, and a stigma of about equal length, characteristics usually associated with moth-pollinated plants. In order to extract nectar from this plant, the carpenter bees alight on the flowers, curving the stamens and stigma beneath and forward by means of the abdomen, bite the corolla tube and insert the tongue, which is then pushed forward making a fine longitudinal slit to the base of the tube where the nectar is available.

Table 1. Sample of *Xylocopa darwini* females working *Geoffroea striata,* 8:20 a.m., Floreana Island, 17 February 1964, elevation 150 meters.

	Wings Intact	Wings with Tips Slightly Worn	Wings Frayed	Totals
Collecting pollen (pollen on legs)	6	4	5	15
Taking nectar (pollen on venter only)	5	2	2	9
Totals	11	6	7	24

The whole process is so rapid that it is difficult to observe in detail. Although carpenter bees were seen at *Clerodendron* at various times of day, only once was it convenient to observe the change from bees to moths at the end of the day. Over a 2-hour period beginning at 5 p.m. (on an overcast day), observations were made of insect activity about two large plants in full bloom. At 5 p.m., five female carpenter bees were taking nectar; at 5:20 p.m., four; at 5:40 p.m., two; at 5:52 p.m., only one; and the latest individual left at 5:56 p.m. By 6 p.m. geometrid and noctuid moths were visiting the flowers (the sun set at 6:05), by 6:20 sphinx moths were active, by 6:30 it was too dark to see insect activity without a light. At 7 p.m. when observations were terminated moth activity was fairly intense, although it could not be determined whether they were successfully extracting nectar from flowers already visited by carpenter bees. In this instance bee activity terminated abruptly just before sunset—perhaps because the sky was obscured by overcast—and then the moths took over. In other situations, carpenter bees were seen in flight after sunset but there was no opportunity to determine whether or not they are active on warm, clear, moonlight nights as has been reported for some other species. Although both sexes of carpenter bees visit *Clerodendron* for nectar, males do so primarily near midday, when they are extremely active, and they could not be approached closely enough to see whether they slit flowers in the manner of the female or visited flowers which had already been slit. However, at Tortuga Bay, where the endemic *Periloba galapagensis,* which also has a deep, tubular corolla, was under observation, both sexes visited the flowers and males were seen puncturing the corolla (Rick, 1966; also, see Fig. 1).

Intensity of pollen-collecting activity about plants which produce pollen acceptable to *Xylocopa* not only varied, as would be expected,



Explanation of Figures

Fig. 1. Upper: *Xylocopa darwini* Cockerell, female (left), male (right), approximately twice natural size. Lower: Male *X. darwini* puncturing corolla of *Periloba galapagensis* in order to gain access to nectar, Tortuga Bay, Santa Cruz Island (C. M. Rick).

Table 2. Sample of *Xylocopa darwini* females working *Sida paniculata,* 9:00 a.m., Floreana Island, 17 February 1964, elevation 210 meters.

	Wings Intact	Wings with Tips Slightly Worn	Wings Frayed	Totals
Collecting pollen (small amount on legs)	1	5		6
Taking nectar (pollen on venter only)	14	1	1	16
Totals	15	6	1	22

in relation to the time of day when fresh pollen is presented (for example, *Sida angustifolia* and *Sida rhombifolia* (Fig. 2) grow intermixed, but one opens at 7:30 or 8:00 a.m., the other not until midmorning or later; the bees respond accordingly), but also to some extent according to the age and possibly the experience of the bee. For example, of a morning sample of 24 females taken from *Geoffroea striata* at 8:20 a.m. on Floreana Island, 15 were collecting pollen and only six of these were presumably recently emerged (wing tips intact; mandibles unworn, etc.), a number about equal to the recently emerged bees taking nectar only (Table 1). On the other hand, at 9:00 a.m., of a sample of 22 females taken from *Sida paniculata,* 16 were presumably recently emerged, and only six in various age categories were gathering pollen (Table 2). A sample from *Prosopis dulcis,* taken in the late afternoon when one would expect pollen collecting to be tapering off and nectar-taking activity high, yielded results similar to those from *Geoffroea* (Table 3).

Table 3. Sample of *Xylocopa darwini* (both sexes) from *Prosopis dulcis,* 4:00–5:00 p.m., Floreana Island, 17 February 1964, elevation 50 meters.

	Wings Intact	Wings with Tips Slightly Worn	Wings Frayed	Totals
♂♂ taking nectar (pollen on venter)	4	5	4	13
♀♀ collecting pollen (loads smaller than in a.m.)	6	2	2	10
♀♀ taking nectar (pollen on venter only)	8	6	5	19
Totals	18	13	11	42

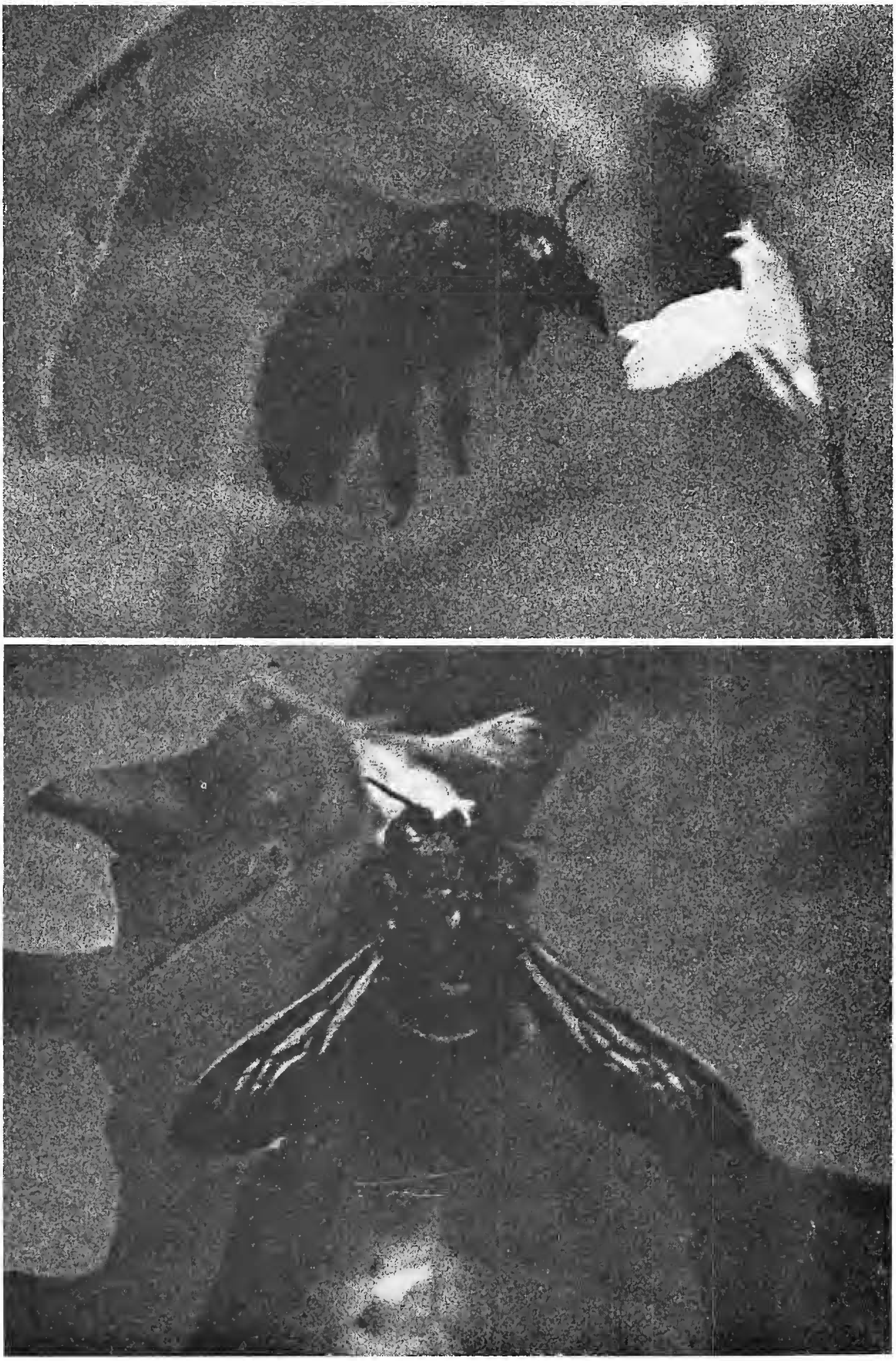
EXPLANATION OF FIGURES

Fig. 2. Two views of a female *Xylocopa darwini* gathering pollen from *Sida rhombifolia*, Bella Vista, Santa Cruz Island (D. Q. Cavagnero).

Among the vine-type legumes, two pollen sources actively worked in the latter part of the morning in the Transition Zone of Santa Cruz are *Galactea jussiana* var. *volubilis* and *Rhynchosia minima.* The former is pink-flowered and climbs over lava and bushes but the flowers are hidden below and must be searched out below. They are small (about 15 mm long) but they hang from well-supported peduncles which hold the weight of the bee easily. The latter is yellow-flowered and also grows over bushes but the flowers are exposed from above, and although even smaller than those of *Galactea* they are quite conspicuous, being arranged in series. When visited by the carpenter bee the stem usually bends to the underlying foliage to support the bee. Bees working *Galactea* had large pollen loads, those at *Rhynchosia* quite small loads. The bees visiting these and other low-growing plants fly and forage close to the ground far below the forest canopy. This is in marked contrast to their activity around large trees and about such tree legumes as *Geoffroea jussiana* and *Prosopis dulcis,* which they approach and leave near treetop level, and are consequently difficult both to observe closely and to capture. Nevertheless, on Floreana, low-growing *Geoffroea* and *Prosopis* yielded good samples (Tables 1, 3).

When visiting *Passiflora foetida* for nectar, which the Galápagos carpenter bee does early in the morning [unlike the Hawaiian carpenter bee which visits the passion fruit, *Passiflora edulis* f. *flavicarpa,* in the afternoon when the flowers begin to open at about 1 p.m. (Nishida, 1963)], the dorsum becomes heavily dusted with pollen, a fact which may be recognized at a distance of several yards. The same is true of bees which visit flowers of the tree cactus, *Opuntia echios,* as they burrow into the flower among the anthers. When visiting *Justicia galapagana,* the bees alighting on the flowers brush the stamens with the head and thus carry considerable pollen from each flower (Fig. 3). As they elevate the legs to brush pollen on them, the head touches the stigma.

With regard to the native Galápagos cotton (*Gossypium barbadense* var. *darwinii*), the role of the carpenter bee in pollination is not well understood. However, recently acquired information concerning nectaries of the latter hints as to its pollination relations (Stephens, unpublished). Observations in the field and on cultures grown from seeds collected in the wild reveal that nectaries (extrafloral, as well as foliar) may vary from near absence to a degree of development approximating that in cultivated *G. barbadense.* This entire range in nectary development has been found in populations on San Cristóbal and Floreana. Reduced nectaries also characterize *G. tomentosum* endemic to Hawaii (Stephens, 1964) and forms of *G. hirsutum* on



Explanation of Figures

Fig. 3. Upper: Female *Xylocopa darwini* approaching flower of *Justicia galapagana* with pollen on the head. Lower: Female visiting *Justicia* flower, bending it downward and touching stamens and stigma with head (C. M. Rick).

Table 4. Summary of flower records for *Xylocopa darwini*, 20 January–28 February 1964.

Family	Species	Sites	Nature of Visits	Level of Activity
Cannaceae	*Canna* sp.	Santa Cruz Is.: Forest Zone above Academy Bay	Not determined	Moderate
Nyctaginaceae	*Boerhaavia scandens*	Santa Cruz Is.: Arid, Transition Zones above Academy Bay	Mainly nectar, some pollen	Intense; bees very numerous
	Mirabilis jalapa	Santa Cruz Is.: Academy Bay	Nectar, pollen	Moderate
Portulacaceae	*Portulaca oleracea*	Santa Cruz Is.: Acad. emy Bay to Transition Zone	Not determined	Very low
Lauraceae	*Persea gratissima*	Santa Cruz Is.: Forest Zone above Bella Vista	Pollen (?), nectar	Moderate
Cruciferae	*Brassica campestris*	Floreana Is.: Moist Forest nr. Saddle Point	Nectar, pollen	Low
Leguminosae	*Acacia macracantha*	Santa Cruz Is.: Academy Bay, Arid Zone	Pollen, nectar	Low to moderate
		Florcana Is.: Black Beach to Saddle Point	Pollen, nectar	Moderate to intense
	Acacia tortuosa	Santa Cruz Is.: Academy Bay	Pollen, nectar	Moderate
	Cassia occidentalis	Santa Cruz Is.: Transition Zone above Academy Bay	Not determined	Low at midmorning
	Crotolaria setifera	Santa Cruz Is.: Transition Zone above Academy Bay	Not determined	Low
	Galactea jussiana	Santa Cruz Is.: Transition Zone above Academy Bay	Pollen, nectar	Moderate to intense
	Geoffroea striata	Floreana Is.: 100–200 m above Black Beach	Pollen, nectar	Intense; bees very numerous
	Inga edulis	Santa Cruz Is.: Forest Zone above Bella Vista	Pollen, nectar	Intense
		Floreana Is.: Moist Forest nr. Saddle Point	Pollen, nectar	Intense
	Parkinsonia aculeata	Santa Cruz Is.: Academy Bay	Pollen, nectar	Moderate

Table 4. Continued.

Family	Species	Sites	Nature of Visits	Level of Activity
		Floreana Is.: Black Beach	Pollen, nectar	Moderate
		Española Is.: East end	Not determined	Low
Leguminosae	*Prosopis dulcis*	Santa Cruz Is.: Academy Bay	Pollen, nectar	Moderate
		Floreana Is.: Black Beach	Pollen, nectar	Intense; bees very numerous
	Rhynchosia minima	Santa Cruz Is.: Transition Zone above Academy Bay	Pollen, nectar	Intense
Zygophyllaceae	*Tribulus cistoides*	Santa Cruz Is.: Academy Bay	Not determined	Low
Simarubaceae	*Castela galapageia*	Santa Cruz Is.: Academy Bay; Arid Zone to 300 m.	Pollen, nectar	Intense
Burseraceae	*Bursera graveolans*	Santa Cruz Is.: Academy Bay to Transition Zone	Pollen, nectar	Moderate to intense
		Floreana Is.: Black Beach	Pollen, nectar	Moderate
Sapindaceae	*Cardiospermum galapageum*	Santa Cruz Is.: Academy Bay	Pollen, nectar	Moderate
Malvaceae	*Abutilon depauperatum*	Santa Cruz Is.: Transition Zone above Academy Bay	Pollen, nectar	Moderate
	Bastardia viscosa	Santa Cruz Is.: Arid Zone nr. Academy Bay	Pollen, nectar	Moderate
	Gossypium barbadense var. *darwinii*	Isabela Is.: Tagus Cove	Nectar	Low
	Hibiscus manihot	Santa Cruz Is.: Forest Zone above Bella Vista	Nectar	Moderate
	Hibiscus tiliaceus	Santa Cruz Is.: Academy Bay	Nectar	Intense
	Malvastrum coromandelianum	Santa Cruz Is.: Transition Zone above Academy Bay	Pollen, nectar	Moderate
	Sida acuta	Santa Cruz Is.: Transition Zone above Academy Bay	Pollen, nectar	Moderate to intense
	Sida angustifolia	Santa Cruz Is.: Transition Zone above	Pollen, nectar	Moderate to intense

Table 4. Continued.

Family	Species	Sites	Nature of Visits	Level of Activity
		Academy Bay		
		Floreana Is.: 200–300 m above Black Beach	Pollen, nectar	Moderate
Malvaceae	*Sida paniculata*	Floreana Is.: 200–290 m above Black Beach	Pollen, nectar	Intense; bees very numerous
	Sida rhombifolia	Floreana Is.: 200–300 m above Black Beach	Pollen, nectar	Moderate
Sterculiaceae	*Waltheria reticulata*	Santa Cruz Is.: Arid Zone above Academy Bay	Nectar	Moderate
Passifloraceae	*Passiflora foetida*	Santa Cruz Is.: Vicinity of Academy Bay	Pollen, nectar	Intense
Loasaceae	*Mentzelia aspera*	Santa Cruz Is.: Arid Zone nr. Academy Bay	Pollen, nectar	Moderate
Cactaceae	*Opuntia echios*	Santa Cruz Is.: Academy Bay to Transition Zone	Pollen, nectar	Moderate
	Opuntia megasperma	San Cristóbal Is.		
Myrtaceae	*Psidium guayava*	Floreana Is.: Moist Forest nr. Saddle Point	Pollen, nectar	Intense
		San Cristóbal Is.		
Melastomaceae	*Miconia robinsoniana*	Santa Cruz Is.: Upper Zone between Bella Vista and Cerro Camote	Nectar	Moderate
Apocynaceae	*Vallesia glabra*	Santa Cruz Is.: Academy Bay nr. beach	Not determined	Low
Convolvulaceae	*Ipomoea pes-caprae*	Santa Cruz Is.: Academy Bay, sandy beach	Nectar	Low
Boraginaceae	*Cordia lutea*	Santa Cruz Is.: Academy Bay and vicinity	Nectar (?)	Very low
Verbenaceae	*Clerodendron molle*	Santa Cruz Is.: Academy Bay to Upper Transition Zone	Nectar	Moderate to intense
	Lantana peduncularis	Santa Cruz Is.: Academy Bay	Nectar	Moderate

Table 4. Continued.

Family	Species	Sites	Nature of Visits	Level of Activity
Verbenaceae	*Stachytarpheta cayannensis*	Floreana Is.: Edge of Moist Forest nr. Saddle Point	Nectar	Moderate
Nolanaceae	*Periloba galapagensis*	Santa Cruz Is.: Tortuga Bay, beach	Pollen, nectar	Intense
Solanaceae	*Physalis pubescens*	Santa Cruz Is.: Academy Bay	Nectar	Low
Scrophulariaceae	*Bacopa monniera*	Santa Cruz Is.: Upper Arid and Transition Zones above Academy Bay	Nectar	Moderate
Acanthaceae	*Justicia galapagana*	Santa Cruz Is.: Transition and Forest Zone nr. Bella Vista	Pollen, nectar	Intense
	Tetramerium hispidium	Santa Cruz Is.: Vicinity of Academy Bay	Not determined	Low
Rubiaceac	*Chiococca alba*	Santa Cruz Is.: Vicinity of Academy Bay	Nectar	Low
	Coffea arabica	Santa Cruz Is.: Forest Zone above Bella Vista	Nectar	Moderate
	Psychotria rufipes	Santa Cruz Is.: Forest Zone above Bella Vista	Pollen, nectar	Intense
Cucurbitaceae	*Cucurbita pepo*	Santa Cruz Is.: Forest Zone above Bella Vista	Pollen, nectar	Moderate
	Momordica indica	Santa Cruz Is.: Transition Zone above Academy Bay	Nectar	Low
Goodeniaceae	*Scaevola plumieri*	Floreana Is.: Black Beach	Nectar	Low
Compositae	*Bidens pilosa*	Floreana Is.: Edge of Moist Forest nr. Saddle Point	Nectar	Low
	Macraea laricifolia	Floreana Is.: 100 m above Black Beach	Nectar	Low
	Scalesia affinis	Santa Cruz Is.: Upper Arid Zone above Academy Bay	Pollen, nectar	Moderate to intense
		Floreana Is.: Vicinity of Black Beach	Pollen, nectar	Low to moderate
	Scalesia sp.	Santa Cruz Is.: Darwin Research Station; Puerto Nuñez	Pollen, nectar	Low to moderate

Table 4. Continued.

Family	Species	Sites	Nature of Visits	Level of Activity
Compositae	*Scalesia helleri*	Santa Cruz Is.: Tortuga Bay	Pollen, nectar	Low to moderate
		Santa Fé Is.: Cliffs above Barrington Cove	Pollen, nectar	Low
	Scalesia pedunculata	Floreana Is.: Forest Zone nr. Saddle Point	Pollen, nectar	Low to moderate
		Santa Cruz Is.: Forest Zone above Bella Vista	Pollen, nectar	Low to moderate

various Pacific islands. Although the significance of these observations is not entirely clear, they suggest evolutionary stages in the elimination of nectaries. In such insular habitats a deficiency or lack of insect pollinators might possibly have resulted in reduced selection pressure to retain nectaries.

POSSIBLE ROLE OF THE CARPENTER BEE IN THE ESTABLISHMENT AND EVOLUTION OF THE GALÁPAGOS FLORA

At the present time, the Galápagos carpenter bee occurs on all major islands in the archipelago and in all vegetational zones from littoral to the Miconia forest, visiting small flowers and large, weedy adventives and endemics, plants which present their pollen or nectar at sunrise, others which have food available at sunset.

However, since the bees require nectar for their own sustenance, nectar and pollen for their young, and wood in which to nest, they could not have been permanently established in the Galápagos until woody plants were present which either produced sufficient nectar and pollen to sustain the species, or were growing among flowering plants that did. In the case of butterflies and hawkmoths, both an abundance of nectar and appropriate larval food plants would have been a prerequisite to establishment, thereby demanding a more diverse flora than necessarily would have been required by the carpenter bee, and taxonomic evidence suggests that they are more recent arrivals (Linsley, 1966).

Rick (1966) made pollination tests on 18 native species of flowering plants in the vicinity of Academy Bay, Santa Cruz Island. He considered results with four of these species to be inconclusive, but flowers of 13 proved capable of automatic self-pollination and the remaining species was demonstrated to be self-compatible but apparently not automatically selfed. Although this sample was small, the absence of any evidence for self-incompatibility and the lack of dependence on insect visits contrast with general pollination relations known of other species in the tested families. This is consistent with the principle expressed by Baker (1955) relative to self-compatibility and establishment after long-distance dispersal. Flowers of nine of the tested species were visited by the only species of bee known to be native, *Xylocopa darwini*; birds and possibly flies and moths accounted for the pollination of two; he found no pollinators for the remainder. Many of these are woody plants suitable for carpenter bee nesting and they produce nectar and/or pollen acceptable to the bees. However, most are small-flowered or drab. Not being dependent upon cross-pollination, their flowers have not been selected for the attraction of insects. We take this as evidence that they preceded the bees on the islands.

On the other hand, the abundance of weedy plants and other adventives suggests that they were established wth ease, and their general attractiveness to the carpenter bees indicates that the bees may have helped materially or accelerated the process of establishment (butterflies and hawkmoths have probably helped to some extent also). This obviously applies to those plants requiring cross-pollination among species deliberately introduced by man, including various agricultural crops, since honeybees are absent.

It is of interest in this connection to compare the proportion of endemic species among the plants in the observed list of plants visited by *X. darwini* (27 per cent of those in Table 4) with that in the Galápagos flora as a whole (41 per cent of the species listed by Stewart, 1911). A test of significance applied to the deviations from values expected from a 2 × 2 contingency table of these two sets of data yields a χ^2 of 4.08 with a probability of 0.02 to 0.05 that such a deviation could result solely from random distribution. Since the regions sampled were exceptionally rich in endemic species, the difference cannot be attributed to a bias of sampling against endemics. In our estimation, it most likely reflects a preference of the bees for the non-endemic plant species.

We tentatively conclude, therefore, that the Galápagos carpenter bee probably played a greater role in the establishment of immigrant plant species than of ancestors of the older endemic species and that evolution among at least some of the endemic elements could have taken place without the aid of the carpenter bee. More definite conclusions must await more definitive information on the taxonomic status of the Galápagos carpenter bee and data indicating to what extent immigrant elements in the Galápagos flora are actually dependent upon insects for cross-pollination.

ACKNOWLEDGMENTS

The authors wish to express their appreciation to the University of California and the National Science Foundation (through grant GE-2370) for the opportunity to participate in the Galápagos International Scientific Project (during January and February 1964). We are also indebted to the Charles Darwin Foundation for assistance in the field, as well as to various colleagues on the project for aid in various ways, especially Ira Wiggins of Stanford University, who not only made or confirmed most of the plant identifications but also noted a number of important observations on carpenter bee–plant relationships. Herbert F. Baker, Director, Botanical Garden, and Paul D. Hurd, Jr., authority on carpenter bees, both of the University of California, Berkeley, lent much encouragement to us in relation to this and related projects. Finally, we acknowledge the assistance of Mr. David Q. Cavagnero who kindly provided us with photographs of the carpenter bee visiting *Sida*.

LITERATURE CITED

BAKER, H. F. 1955. Self-compatibility and establishment after long distance dispersal. Evolution, 9: 347–349.

COCKERELL, T. D. A. 1926. Descriptions and records of bees—CXI. Ann. Mag. Nat. Hist., (9) 17: 657–665.

GARTH, J. S. 1933. Insects. *In* Banning, G. H., Hancock Expedition of 1933 to the Galápagos Islands. Bull. Zool. Soc. San Diego, 10: 18–20.

HURD, P. D., JR. 1958a. Observations on the nesting habits of some New World carpenter bees with remarks on their importance in the problem of species formation. Ann. Entomol. Soc. Amer., 51: 365–375, 5 figs.

1958b. The carpenter bees of the Eastern Pacific Oceanic Islands. Jour. Kansas Entomol. Soc., 31: 249–255.

HURD, P. D., JR., AND J. S. MOURE. 1963. A classification of the large carpenter bees (Xylocopini). Univ. Calif. Publ. Entomol., 29: 1–365, 244 figs.

LINSLEY, E. G. 1966. Pollinating insects of the Galápagos Islands. *In* Bowman, R. I. (Ed.), The Galápagos: Proceedings of the Galápagos International Scientific Projcct. Univ. Calif. Press, Berkeley–Los Angeles. (In press).

MALYSHEV, S. J. 1931. Lebensgeschichte der Holzbienen, *Xylocopa* Latr. Zeitschr. Morphol. Ökol. Tiere (A) 23: 754–809, 15 figs.

NISHIDA, T. 1963. Ecology of the pollinators of passion fruit. Tech. Bull. Hawaii Agr. Exp. Sta., no. 55. 38 p., illus.

PERKINS, R. C. L. 1899. Hymenoptera Aculeata. Fauna Hawaiiensis, 1: 1–115.

RICK, C. M. 1963. Biosystematic studies on Galápagos tomatoes. Occ. Pap. Calif. Acad. Sci., 44: 59–77.

1966. Some plant-animal relationships in the Galápagos Islands. *In* Bowman, R. I. (Ed.), The Galápagos: Proceedings of the Galápagos International Scientific Project. Univ. Calif. Press, Berkeley–Los Angeles. (In press).

SMITH, F. 1877. Hymenoptera and Diptera. *In* Gunther, Account of the Zoological collection made during the visit of H.M.S. "Peterel" to the Galápagos Islands, VIII. Proc. Zool. Soc. London, 1887: 82–84.

STEPHENS, S. G. 1964. Native Hawaiian cotton (*Gossypium tomentosum* Nutt.) Pacific Science, 18: 385–398.

STEWART, A. 1911. A botanical survey of the Galápagos Islands. Proc. Calif Acad. Sci., (4) 1: 7–288.

WILLIAMS, F. X. 1926. The bees and aculeate wasps of the Galápagos Islands. Proc. Calif. Acad. Sci., (4) 2: 347–357.

Observations on *Dioxys productus productus* (Cresson) as a parasite of *Anthidium utahense* Swenk

(Hymenoptera : Megachilidae)

ELBERT R. JAYCOX[1]
University of Illinois, Urbana

Bees of the genus *Dioxys* are "parasites," or depredators of larval food, of several genera of megachilid bees, including *Anthidium*, *Megachile*, and *Osmia* (Hurd, 1958). The biology of the genus is not well known although *Dioxys* adults have been observed in the field and reared from nests of their hosts (Newberry, 1900; Hicks, 1929). In 1962, I observed *Dioxys* females visiting nests of *Anthidium utahense* Swenk at North Logan, Utah, and later obtained adults from the nests. The following observations are offered as an addition to our knowledge of the biology of these bees.

Female *Anthidium utahense* nest in the ground in holes and crevices, frequently using cavities made by other insects and animals. They readily accept artificial nest cavities which offer vertical holes at ground level. I used short lengths of 2- by 4-inch lumber drilled with holes 1 to 3 inches apart along one of the narrow sides and buried so that this side was even with the surface of the ground. Soda straws 6.5 and 7.5 mm in diameter and 70 to 75 mm long were inserted in the holes to facilitate removal of completed nests. Blocks of wood so prepared were

---

[1] Associate Professor of Apiculture. These observations were made while the author was employed by the U. S. Department of Agriculture, Wild Bee Pollination Investigations, Utah State University, Logan, Utah, in cooperation with the Utah Agricultural Experiment Station.

THE PAN-PACIFIC ENTOMOLOGIST 42: 18–20. January 1966